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Running head: Stream insect diversity and abundance in different climatic regions

# Subtropical streams harbour higher genus richness and lower abundance of insects compared to boreal streams, but scale matters

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## Abstract

**Aim:** Biological diversity typically varies between climatically different regions, and regions closer to the equator often support higher numbers of taxa than those closer to the poles. However, these trends have been assessed for a few organism groups, and the existing studies have rarely been based on extensive identical surveys in different climatic regions.

**Location:** We conducted standardised surveys of wadeable streams in a boreal (western Finland) and a subtropical (south-eastern Brazil) region, sampling insects identically from 100 streams in each region and measuring the same environmental variables in both regions.

**Taxon:** Aquatic insects

**Methods:** Comparisons were made at the scales of local stream sites, drainage basins and entire regions. We standardised the spatial extent of the study areas by resampling regional richness based on subsets of sites with similar extents. We examined differences in genus richness and assemblage abundance patterns between the regions using graphical and statistical modelling approaches.

**Results:** We found that while genus accumulation and rank-abundance curves were relatively similar at the regional scale between Finland and Brazil, regional genus richness was higher in the latter but regional abundance much higher in the former region. These regional patterns for richness and abundance were reproduced by basin and local genus richness that were higher in Brazil than in Finland, and assemblage abundance that was much higher in Finland than in Brazil. The magnitude of the difference in genus richness between Brazil and Finland

tended to increase from local through basin to regional scales.

**Main conclusions:** Our findings suggest that factors related to evolutionary diversification might explain differences in genus richness between these two climatically different regions, whereas higher nutrient concentrations of stream waters might explain the higher abundance of insects in Finland than in Brazil.

**Keywords**

alpha diversity, latitudinal diversity gradient, nutrients, rank abundance, regional diversity, stream insects, low-high latitude comparison

# INTRODUCTION

Biological diversity typically varies among climatically different regions, with regions closer to the equator often harbouring higher numbers of species than those at higher latitudes (Rosenzweig, 1995; Gaston, 2000). This latitudinal gradient in species richness is evident for terrestrial organisms such as vascular plants, butterflies, birds and mammals (Hillebrand, 2004a). It has also been found for marine (Hillebrand, 2004b) and freshwater organisms (Pearson & Boyero, 2009). However, there are also notable exceptions to the latitudinal richness gradient among microbes and invertebrates, to name two highly diverse organism groups (Kouki *et al*., 1994; Willig *et al*., 2003; Boulton *et al*., 2008; Soininen, 2012). Studies on many infrequently studied groups of organisms have rarely used extensive standardised surveys (Vinson & Hawkins, 2003; Pearson & Boyero, 2009). These methodological issues may complicate the examination of the drivers of regional and local richness, although there are successful classical (Stout & Vandermeer, 1975; Lake *et al*., 1994) and more recent examples (Dias *et al*., 2014; McCreadie *et al*., 2017). In general, regional differences in richness may stem from differences in spatial extent, evolutionary diversification, current and past climates, productivity or history (Willig *et al*., 2003; Mittelbach *et al*., 2007), whereas local richness gradients may result from differences in biological interactions and abiotic ecosystem features between geographical regions (Vinson & Hawkins, 2003; Heino, 2011).

Stream-dwelling insects are a suitable model group for examining biodiversity patterns between climatically different regions. They comprise many taxonomic orders, of

which mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera), beetles (Coleoptera) and true flies (Diptera) dominate stream insect assemblages in terms of abundance and richness over the world (Vinson & Hawkins, 1998; Lancaster & Downes, 2013). Stream insect richness exhibits various patterns along latitudinal gradients, both at regional (Boyero, 2002; Pearson & Boyero, 2009) and local scales (Stout & Vandermeer, 1975; Jacobsen *et al*., 1997; Vinson & Hawkins, 2003; Boyero *et al*., 2011b). While some insect groups (e.g. dragonflies and beetles) are more diverse in tropical than in northern regions (Brown, 1981; Pearson & Boyero, 2009), other groups (e.g. mayflies, stoneflies and caddisflies) have also diversified extensively in mid-latitude regions (Illies, 1965; Ward, 1992). The reasons for such anomalous latitudinal patterns may relate to the possibility that many taxa of mayflies, stoneflies and caddisflies originated and thus diversified in cold-water streams (Ward, 1992), following the niche conservatism hypothesis (Wiens & Donoghue, 2004). Alternatively, their high diversity in temperate regions may stem from high environmental heterogeneity along seasonal and altitudinal gradients (Vinson & Hawkins, 2003). The latitudinal gradient in the local diversity of stream insects (i.e. species richness within one stream) may be even more complex than that for regional diversity (i.e. total number of species from several streams in a region), as local abiotic conditions may vary strongly even between neighbouring streams (Hynes, 1970; Allan & Castillo, 2007; Boulton *et al*., 2008). Such high variation in local conditions dictates that streams close to each other may harbour insect assemblages differing highly in richness, abundance and composition (Grönroos & Heino, 2012; Landeiro *et al*., 2012). Therefore, although regional-scale stream insect diversity may differ (Brown, 1981; Pearson & Boyero, 2009), among-region differences in local diversity may be less clear (Heino *et al*., 2003; Vinson & Hawkins, 2003;

117 McCreadie *et al*., 2017).

118 Biological diversity at regional and local scales can be studied by using both graphical
119 pattern-based (Magurran, 2004) and modelling approaches (Legendre & Legendre, 2012).
120 Pattern-based approaches include taxon accumulation curves (Ugland *et al*., 2003) and rank-
121 abundance distributions (Whittaker, 1965), both applicable at regional and local scales. For
122 example, there were only slight differences in the taxon accumulation curves among three
123 high-latitude regions (Heino *et al*., 2015b). Taxon accumulation curves have also been used
124 at local scales, where the accumulation curves of temperate stream insects reached an
125 asymptote much earlier than those of tropical streams (Stout & Vandermeer, 1975). Rank-
126 abundance distributions have rarely been applied in stream insect studies at both regional and
127 local scales, but they show a great potential for between-systems comparisons in other
128 contexts (McGill *et al*., 2007). For example, rank-abundance distributions may reveal
129 whether tropical and boreal regions harbour regional assemblages with different degrees of
130 rarity and commonness. Such differences in rarity and commonness may be due to different
131 degrees of ecological specialization, with tropical taxa being more specialized than those at
132 high latitudes (Mittelbach *et al*., 2007; Coley & Kursar, 2014).

133 Modelling approaches have been used extensively to examine how different predictor
134 variables affect variation in biological diversity among regions and among sites (Legendre &
135 Legendre, 2012). For example, based on a comparative analysis of 61 datasets from around
136 the world, Heino *et al*. (2015a) found that stream insect assemblages were more strongly
137 related to the environment than to space, and that the explanatory power of these predictors
138 was low with no obvious latitudinal trend. In a global analysis of local stream insect genus

139 richness, Vinson and Hawkins (2003) found that linear models based on large-scale climatic
140 and energy variables could explain some variation in local richness. They also found no clear
141 latitudinal gradients in the local genus richness of mayflies, stoneflies and caddisflies, but
142 instead that richness showed multiple peaks and often peaked at mid-latitudes. These two
143 studies, although based on large compilations of datasets, are likely to be limited by different
144 sampling methods as well as distinct environmental and spatial extents in different regions.
145 This might hinder firm conclusions on whether stream insect assemblages in tropical,
146 temperate and boreal regions show differences in richness and abundance patterns. For
147 instance, differences in spatial extent may complicate among-region comparisons because
148 larger study areas exhibit larger environmental heterogeneity, thereby affecting diversity
149 estimates (Chase & Knight, 2013). This issue has been considered in previous local-scale
150 studies by using a long-term sampling approach (Vinson & Hawkins, 2003) and in some
151 regional-scale studies by factoring out the effects of spatial extent (Pearson & Boyero, 2009).

152 To overcome some of the problems that have affected comparative studies based on
153 datasets produced by different methods (e.g. Nakagawa & Parker, 2015) and complement
154 previous findings on global gradients (e.g. Pearson & Boyero, 2009), we conducted identical
155 surveys of wadeable streams in a boreal (western Finland) and a subtropical (south-eastern
156 Brazil) region. We believe that broad-scale studies (e.g. based on gridded data) and
157 comparative studies (i.e. based on standardised sampling protocols) are complementary and
158 offer the possibility to test for patterns using different lines of evidence. Thus, by focusing on
159 two regions, as opposed to previous studies that addressed global gradients, we could take
160 detailed and standardised insect samples from 100 streams in each region and measured the
161 same environmental variables in both regions. We also standardised the extent of the study

area by resampling sites from similar-sized areas in both regions. Our specific aims were threefold. We first (i) examined whether genus accumulation curves differed between the boreal and subtropical regions. We expected that there would be faster accumulation of genera in Brazil than in Finland because alpha and beta diversities are typically higher in the tropics (Soininen *et al*., 2007). We also (ii) studied whether rank-abundance distributions differed between Brazil and Finland, with the expectation that there would be many more relatively rare genera in the subtropical than in the boreal region, which is more dominated by a few abundant genera (Brown, 2014). Finally, in addition to these aims, we (iii) modelled variation in local genus richness and local assemblage abundance of stream insects in relation to region identity, while controlling for the effects of key local environmental variables. If evolutionary diversification (Willig *et al*., 2003; Brown, 2014) is contributing to the latitudinal richness gradient, insect genus richness and assemblage abundance should be higher in subtropical than in boreal streams after controlling for the influence of local environmental variables and spatial extent.

# MATERIALS AND METHODS

## Study areas

**Western Finland**. Study sites were located between latitudes 60°41'N and 65°12'N, with spatial extents of ca. 500 km and 300 km in north-south and in east-west directions,

183 respectively (Supporting Information, Fig. S1). The catchments were covered by different
184 land uses, from ones dominated by agriculture to those covered almost entirely by boreal
185 forests (dominated by *Pinus sylvestris* and *Picea abies*). The 100 perennial streams were
186 selected from 20 major river basins, i.e., five separate streams draining into each of 20 boreal
187 rivers were surveyed. Western Finland has the four seasons characteristic of the boreal
188 region: (1) winters lasting from November to March, (2) spring periods in April and May, (3)
189 summers between June and August, and (4) autumn periods generally in September and
190 October. Given the large latitudinal extent, temperature and rainfall vary substantially in the
191 study area. The stream sites were sampled in September 2014. These streams did not
192 experience heavy floods or droughts just before sampling and ranged from pristine forest
193 streams to agricultural streams with little pollution.

194

195 **South-eastern Brazil**. Study sites were located in the State of São Paulo, between latitudes
196 24°38'S and 23°82'S, with spatial extents of 70 km in north-south and 120 km in east-west
197 directions, respectively (Supporting Information, Fig. S1). The 100 perennial streams, with
198 five streams distributed within 20 different catchments as described above, are located
199 between three major Atlantic Forest protected areas (Carlos Botelho, Intervales and Alto
200 Ribeira State Parks). Land cover varied among catchments, with some dominated by
201 agriculture (mainly pastures, and *Eucalyptus* and *Pinus* plantations) to some entirely covered
202 by Atlantic Forest. This region is characterised by two seasons: a drier season from April to
203 August (average rainfall from 45 to 80 mm per month; average temperature from 16 to 20ºC)
204 and a wetter season from September to March (average rainfall from 105 mm to 180 mm per
205 month; average temperature from 20 to 23ºC). The sites were sampled from September to

206 November in 2015. Streams did not suffer from recent floods or droughts and ranged from
207 pristine forest streams to moderately polluted streams in agricultural areas.

208

209 **Field surveys**

210

211 We measured 15 physical and chemical variables that have been found to be important for
212 stream insect distributions in boreal (Malmqvist & Mäki, 1994; Grönroos & Heino, 2012)
213 and tropical (Siqueira *et al*., 2012; Al-Shami *et al*., 2013) regions. For physical variables, we
214 measured current velocity (m/s) and depth (cm) at 30 (in Finland) and nine (in Brazil)
215 random spots in a riffle site. Particle size classes (%) were visually estimated in 0.25 $m^2$
216 squares at 10 (in Finland) and three (in Brazil) random locations in a riffle site. We used a
217 modified Wenthworth's scale of particle size classes: sand (0.25-2 mm), gravel (2-16 mm),
218 pebble (16-64 mm), cobble (64-256 mm) and boulder (256-1024 mm). Based on the mean
219 estimates for each site, we calculated the Shannon diversity of substratum particle sizes for
220 each stream site. We also measured mean stream width of the sampling site based on 10 (in
221 Finland) and three (in Brazil) cross-channel measurements and visually estimated shading
222 (i.e. canopy cover) by riparian vegetation at each sampling site. We used satellite images to
223 estimate native forest cover within a 400-m buffer along tracts of the sampled streams. For
224 chemical variables, we measured pH and conductivity at each site in the field using YSI
225 device model 556 MPS (YSI Inc., Ohio, USA) in Finland and Horiba device U-50 series in
226 Brazil. Water samples were analysed for total nitrogen (TN) and total phosphorus (TP)
227 following national standards for Finland (Finnish Board of Waters and the Environment

228 1981) and Brazil (Golterman *et al*., 1978; Mackereth *et al*., 1978).

229 We took a 2-minute kick-net sample (net mesh size: 0.5 mm) at each of the stream
230 sites surveyed in Finland and Brazil. The sample for each site consisted of four 30-seconds
231 sample units that were obtained in the main microhabitats (i.e. considering variations in
232 current velocity, depth, particle size and macrophyte cover) at a riffle site of c. 25 to 50 $m^2$.
233 The four sample units were pooled, preserved in alcohol in the field and taken to the
234 laboratory for further processing and identification. All insects were separated from debris,
235 and taxa of our interest (Ephemeroptera, Odonata, Plecoptera, Megaloptera, Trichoptera and
236 Coleoptera) were identified to genus level.

237 Species-level identification is mostly not feasible for aquatic insects in Brazil as many
238 species remain undescribed, particularly their aquatic immature stages, and new species are
239 still being discovered in the region (Cruz *et al*., 2013). A previous evaluation on the use of
240 coarse family-level identification in the same Brazilian region as studied here indicated that it
241 produces reliable assessment of stream fauna (Melo, 2005). Species-level identification is
242 more feasible in Finland, but regional, basin and local aquatic insect faunas of wadeable
243 streams are still inadequately known. However, genus richness portrays adequately patterns
244 in species richness in Finnish streams (Heino & Soininen, 2007). Accordingly, we opted to
245 use genus identification to enable direct comparisons between Finland and Brazil.

246

247 **Standardization of sampling effort and spatial extent**

248

249 We developed different procedures to control for variation in sampling effort and differences
250 in spatial extent, before comparing the two regions. We redirect the reader to the
251 supplementary material (see Supporting Information and Fig. S2) for a detailed account of
252 these procedures. These procedures were needed to ensure that between-region differences in
253 richness were not caused by anomalous sites with low densities and by differences in the
254 number of streams within drainage basins and spatial extents.

255

256 **Graphical data analysis at the regional scale**

257

258 To describe regional-scale patterns in the stream insect faunas of Finland and Brazil, we used
259 two graphical approaches using mean values from reduced/standardised datasets. First, we
260 drew genus accumulation curves for each region to see if genus richness accumulated
261 similarly with increasing number of stream sites (Coleman *et al*., 1982). This approach
262 followed the method "exact" devised by Ugland *et al*. (2003). Second, we used genus rank-
263 abundance curves at regional level to show which genera were most abundant in Finland and
264 Brazil. In these plots, abundance (as proportions of total regional abundance) is on the y-axis,
265 and genera are ranked from the most abundant to the least abundant on the x-axis (Whittaker,
266 1965). Genus accumulation curves were drawn using the function 'specaccum' in the R
267 package 'vegan' (Oksanen *et al*., 2013).

268

269 **Modelling genus richness and assemblage abundance across the regions and along**

**environmental gradients**

The standardisation of spatial extent (see Supporting Information) and sample sizes (rarefaction) allowed an improved comparison of genus richness between the regions. However, the streams also differed on several environmental features between the regions. We thus estimated differences in abundance, observed genus richness and rarefied genus richness between the two regions after taking into account the environmental variables described earlier and known to affect stream insect assemblages.

Physical variables were similar between regions (Table 1). In contrast, chemical variables differed between the regions, with conductivity, total phosphorous and total nitrogen being much higher in Finland than in Brazil (Table 1). Accordingly, we standardised chemical variables by their maximum within each region before analyses using the function 'decostand' in the R package 'vegan' (Oksanen *et al*., 2013). The standardisation reduced the correlation with the 'region identity' variable and allowed the evaluation of effects of those variables within the range of variation within each region.

We removed the variable boulder, as the five substrate classes sum to 1, and they would thus be correlated to each other. We then removed collinear environmental variables (i.e. cobble and TN) by sequentially removing those with variance inflation factor (VIF) higher than 2 (Zuur *et al*., 2010). We fitted linear models with 14 explanatory variables: the 13 environmental variables described earlier and 'region identity', our categorical variable of interest. We performed model selection using AIC criterion, although we were most interested in the effect of 'region identity' after partialling out the effect of environmental

variables. The model selection employed aimed to provide a simpler model. We ran separate multiple regressions on rarefied richness, observed richness and assemblage abundance using 14 predictor variables. Finally, we ran a commonality analysis in the context of multiple regression (Seibold & McPhee, 1979; Ray-Mukherjee *et al*., 2014) to infer the unique, common and total contributions of each predictor variable to response variables. VIF analyses were done using the function 'vif' in the 'car' R package (Fox & Weisberg, 2011). Modelling analyses were run using the functions 'lm' and 'step' in the R package 'stats' (R Core Team, 2017) and 'commonalityCoefficients' in the R package 'yhat' (Nimon *et al*., 2015).

# RESULTS

## Patterns of regional-scale richness and abundance

Stream insect abundance and richness showed interesting differences between Finland and Brazil. First, only four genera were shared between Finland and Brazil, these being the mayfly genus *Caenis* and the caddisfly genera *Hydroptila, Oecetis* and *Oxyethira*. Second, total regional abundance was much higher in Finland (total number of insect individuals in 100 streams: 86,048) than in Brazil (16,113), yet regional genus richness ($n$ = 100 streams) was slightly higher in Brazil (83) than in Finland (77).

The 97 paired standardised sets of streams included (see Supporting Information and

313 Fig. S2), on average, 24.5 (min = 17, max = 29) streams in each region, and the average
314 spatial distance among them was 56.0 km (min = 44.1, max = 65.7) in Brazil and 57.6 km
315 (min = 45.3, max = 68.8) in Finland. These results indicate the effectiveness of our
316 standardization protocol. For all standardised pairs, total abundance in the set of streams in
317 Finland was higher than in Brazil (average paired difference = 16,752 individuals). In
318 contrast, observed genus richness was always higher in Brazil and included 40% more genera
319 than in their paired counterparts in Finland (average paired difference = 18.66 genera; Fig.
320 1A). This difference increased to 76% after taking differences in the number of sampled
321 individuals into account (within-pair rarefaction; average paired difference = 28.54 genera;
322 Fig. 1B).

323 Sample-based accumulation curves were similar between Finland and Brazil, although
324 genus richness was much higher in Brazil (Fig. S3A, B). In contrast, individual-based
325 accumulation curves indicated that many more genera would be detected in Brazil with
326 additional sampling (Fig. S3C, D).

327 Rank-abundance curves for Finland and Brazil differed mostly in two aspects (Fig.
328 S4). The two most abundant genera in Finland tended to include much more of the total
329 number of individuals (on average, 32.03 and 19.78%) than the two most abundant in Brazil
330 (14.45 and 12.16%). In contrast, the proportions of rare genera were similar between Brazil
331 (74.5 and 81.6% of the genera with less than 1 and 2% of the total abundance) and Finland
332 (74.5 and 81.8%).

333

334 **Patterns of basin-scale richness and abundance**

335

336 Samples from the 17 basins in Brazil, each including four or five streams, included a total of
337 15,471 individuals. The 19 basins in Finland included 85,050 individuals. Observed genus
338 richness was 31% higher in Brazil than in Finland (37.23 and 28.42, respectively; Fig. 2A).
339 The basin with the lowest abundance was found in Brazil, with 295 individuals. Rarefied
340 genus richness for 295 individuals was 61.3% higher in Brazil than in Finland (30.17 and
341 18.51, respectively; Fig. 2B).

342

343 **Patterns of local-scale richness and abundance**

344

345 The reduced set of streams in Brazil, after removing 12 streams with low insect abundance,
346 included on average 181.5 individuals and 17.84 genera per stream riffle site. The reduced set
347 of streams in Finland included many more individuals (mean = 886.57) and fewer genera
348 (14.01) per stream. Observed mean genus richness per stream was 27% higher in Brazil than
349 in Finland (Fig. 3A). Rarefied genus richness per stream was 64.3% higher in Brazil than in
350 Finland (11.52 and 7.41, respectively; Fig. 3B).

351

352 **Differences in genus richness and assemblage abundance between the regions**

353

354 The reduced model including 'region' and five local environmental variables explained

355 49.6% of the variation in rarefied genus richness (Table 2). Region had the strongest effect on
356 rarefied genus richness, with Brazil possessing more genera per stream after controlling for
357 the effects of local environmental variables. Rarefied genus richness was also higher in wider
358 streams and those with a high proportion of native forest vegetation cover. Proportion of sand
359 in the stream bottom was negatively related to rarefied richness. A similar reduced model for
360 observed richness explained 37.6% of variation, and the most important predictor variables
361 were region and five local variables. Finally, assemblage abundance was best explained by
362 region and seven local variables, and the model accounted for 61% of variation in assemblage
363 abundance (Table 2). Full models can be found in Supporting Information (Table S1).

364 Commonality analysis strengthened the findings of basic linear models by showing
365 that 'region' typically had the highest unique (14.1% to 18.8%) and total (8.5% to 44.2%)
366 effects on rarefied richness, observed richness and assemblage abundance (Table 2). The only
367 exception was for observed richness as stream width had the highest total effect (11.4%). For
368 rarefied richness, shading and forest cover were also relatively important. For observed
369 richness, stream width and forest cover were important in addition to the region effect.
370 Finally, for assemblage abundance, the second and third most important predictors were
371 shading and velocity, respectively.

372

373 # DISCUSSION

374

375 We found that, for the entire datasets, the regional difference in genus richness was

surprisingly small between Brazil (83 genera) and Finland (77 genera) considering that regions closer to the equator usually harbour more diversity than those closer to the poles (Rosenzweig, 1995; Willig *et al*., 2003). While differences between tropical and boreal regions are expected for various groups of organisms, many freshwater organisms do not obey such general 'laws' (Vinson & Hawkins, 2003; Pearson & Boyero, 2009; Heino, 2011; Soininen, 2012). Rather, aquatic insects, such as mayflies, stoneflies and caddisflies, do not often follow typical latitudinal trends in regional diversity, whereas some other aquatic insects, such as dragonflies and beetles, do so (Brown, 1981; Pearson & Boyero, 2009). In our study, mayflies, dragonflies and beetles were regionally more diverse in Brazil than in Finland, whereas the opposite was true for stoneflies and caddisflies (Supporting Information, Fig. S5). This finding suggests that some insect orders may be more diverse closer to the poles than to the equator. We emphasise, however, that the difference in genus richness between Brazil and Finland was much larger after accounting for spatial extent. Indeed, in the reduced standardised datasets, regional genus richness was clearly higher in Brazil than in Finland. This finding underscores the importance of standardising spatial extent when comparing regional richness estimates. Such standardisation is important because larger spatial extent typically incorporates more environmental heterogeneity, resulting in higher richness (Chase & Knight, 2013) and leading to biased between-region comparisons in the case of different spatial extents.

In general, richness tends to be correlated with abundance especially if sampling effort varies between regions (Gotelli & Collwell, 2001; Evans *et al*., 2005). However, this was not the case in our study with identical field sampling designs. Hence, it seems that the very high regional abundance does not lead to high genus richness in Finland, and tropical

399 faunas remain more diverse even when having much lower regional abundances than boreal
400 faunas. Previous studies have detected increasing abundance of stream detritivorous
401 invertebrates with increasing altitude (Yule *et al*., 2009) and latitude (Boyero *et al*., 2011),
402 suggesting that stream insect abundance may be lower in higher temperatures. Also, other
403 differences between regions, such as local stream productivity and other environmental
404 features, affect stream insect abundance (Jacobsen *et al*., 1997; Vinson & Hawkins, 2003). In
405 our study, nutrient concentrations were much higher in Finnish than Brazilian streams (Table
406 1), which might have contributed to higher insect abundance in Finland. This difference
407 might stem from the generally nutrient-poor soils of tropical landscapes (Reich & Oleksyn,
408 2004), as catchment features typically determine stream water chemistry (Soininen *et al*.,
409 2015). However, in the linear models, the effect of nutrients was masked by collinearity with
410 the 'region' variable, the latter of which was the variable of our main interest and forced into
411 all models.

412 Genus accumulation curves differed slightly between the two regions. While the
413 curves in both regions nearly reached an asymptote, the increase of genera was faster in
414 Brazil than in Finland (Fig. S3). Such steeper accumulation curves in the subtropical than in
415 the boreal region might be related to the slightly higher local genus richness in Brazil than in
416 Finland. Working with data from three high-latitude regions (66$^{o}$N to 70$^{o}$N), Heino *et al*.
417 (2015b) found only minor differences in species accumulation curves among the regions,
418 suggesting that environmental differences or species pool characteristics did not contribute to
419 differences in species accumulation. The situation should be different between geographically
420 distant regions, harbouring almost completely different stream biotas, such as those in Brazil
421 and Finland.

Despite differences in regional genus richness and total abundance between Brazil and Finland, the rank-abundance curves were rather similar between the two regions (Fig. S4). The curves were characterised by few common genera and several uncommon to very uncommon genera, a pattern that has previously been found for tropical streams (Siqueira *et al*., 2012). However, the two most common genera in Finland were much more abundant than their counterparts in Brazil. In both study regions, the most common genus belonged to the beetle family Elmidae (*Elmis* in Finland and *Heterelmis* in Brazil). These riffle beetles are typical inhabitants of streams over most of the world, being often common in fast-flowing sites (Elliott, 2008). The second and third most common genera in Finland belonged to mayflies (*Baetis*) and stoneflies (*Nemoura*), whereas those in Brazil belonged to caddisflies (*Smicridea*) and mayflies (*Farrodes*). These insect orders typically dominate stream insect faunas in many parts of the world (Lancaster & Downes, 2013). In general, these results suggest an interesting avenue for further investigations: the existence of a "latitudinal gradient" in niche packing (see also Willig *et al*., 2003).

We also found differences in local genus richness and local assemblage abundance between Finland and Brazil. However, the richness difference between Finland and Brazil was not as strong at the local scale as at the regional scale (compare Fig. 1 and 2 with Fig. 3), which was evidenced by both the entire dataset and the reduced standardised datasets. While local genus richness was higher in subtropical than in boreal streams, local assemblage abundance showed the opposite pattern. However, both richness and abundance also showed considerable variation within each region (Table 1, Fig. 3). These findings suggest that local richness and local abundance in streams are determined by both regional and local factors, and it seems that genus richness benefits from tropical conditions, whereas assemblage

445 abundance benefits from boreal ecological features. Higher genus richness in the tropics
446 might result from ice age history and temperature-related evolutionary rates (Mittelbach *et*
447 *al*., 2007), which should be less important and more important, respectively, in the tropical
448 than in boreal regions (Brown & Lomolino, 1998). For example, previous evidence indicates
449 that Neotropical areas can act both as "museums" (i.e. with old persistent lineages) and as
450 "cradles" (i.e. with new species continuously originating) of insect diversity (Moreau & Bell,
451 2013). In addition, regional factors set the upper limits to local genus richness and
452 assemblage abundance, which are further affected by more localised variation in stream
453 environmental variables (Poff, 1997; Vinson & Hawkins, 2003). These environmental
454 variables may vary within regions (e.g. pH) or differ between regions (e.g. TN), as in our
455 case.

456 An interesting finding was that the between-region richness difference decreased from
457 regional through basin to local scales (40, 31 and 27% for observed genus richness and 76, 63
458 and 55% for rarefied genus richness; Figs 1, 2 and 3). This finding suggests that evolutionary
459 history and climatic influences are strong in setting up differences in regional genus richness
460 (standardized spatial extents), while local genus richness differences are slightly diminished
461 due to the possible operation of catchment variables (acting on catchment-scale) and local
462 environmental variables (acting on stream-scale) with decreasing spatial grain of a study.
463 While previous studies that were based on intensive site-based inventories (Vinson &
464 Hawkins, 2003) or more extensive regional inventories (Pearson & Boyero, 2009) did not
465 adopt standardized methods, they were able to provide broad generalizations on global
466 richness gradients. However, our study adds to previous findings by providing more precise
467 evidence from explicit consideration of variation of richness and abundance across spatial

scales. Hence, our findings emphasize the need to consider both spatial extent and grain of the study when making comparisons of between-region differences in biodiversity patterns (Vinson & Hawkins, 1998; Heino, 2011).

## Conclusions

We found that stream insect genus richness and assemblage abundance differed between our subtropical and boreal regions. Our main finding was that genus richness was higher in Brazil than in Finland (and more so at regional and basin than local scales), yet assemblage abundance was much higher at all spatial scales in Finland than in Brazil. These patterns hold in both entire datasets and in reduced datasets based on resampling of the stream sites from similar-sized areas. Differences in nutrient concentrations and temperature of stream waters might explain the higher abundance of insects in Finland than in Brazil, whereas possibly factors related to evolutionary diversification might explain differences in genus richness between these two regions. Our further studies should shed more light on these issues by focusing on the functional structure and phylogenetic diversity of stream insect faunas in these geographically distinct regions.

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666

667 **DATA ACCESSIBILITY**

668 The data used in this work are stored in PANGAEA (https://www.pangaea.de/). The datasets
669 can also be found in Supporting Information of this paper.

670

671 **BIOSKETCH**

672 Our Finnish-Brazilian team is interested in biodiversity patterns in general and those from
673 stream ecosystems in particular. This research originated during a joint research project
674 funded by the Academy of Finland and FAPESP. Author contributions: JH, JS, TS, ASM,
675 VLL and LMB conceived the ideas; JJM, DKP, KTT, VP and TSFS collected the data; DKP,
676 VSS and KTT identified the insects; ASM analysed the data; and JH and TS led the writing.
677 All authors contributed to the ideas and approved the final version of the manuscript.

678

679 **SUPPORTING INFORMATION**

680 Additional Supporting Information is available in the online version of this paper.

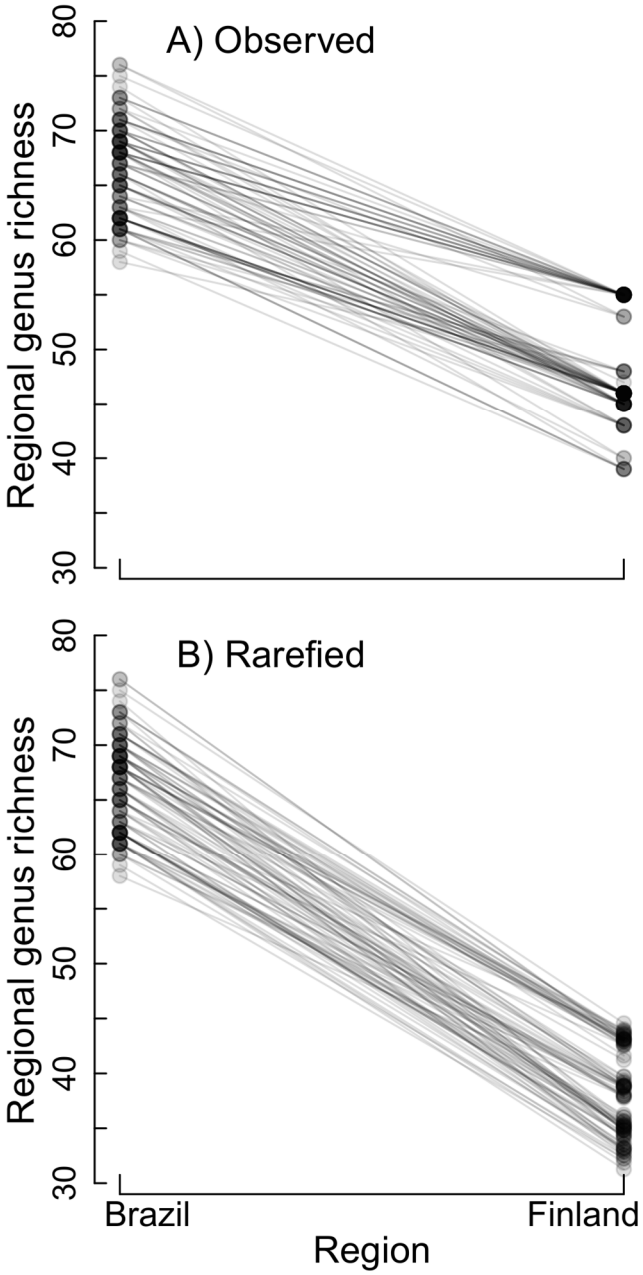
## Tables and Figures

Table 1. Descriptive statistics of local genus richness, local rarefied genus richness and local assemblage abundance, of stream insects, as well as of selected physical and chemical variables measured in streams in Finland (N = 97) and Brazil (N = 88). These values are based on the reduced datasets after removal of anomalous sites. SD = standard deviation, IQR = interquartile range, CV = coefficient of variation.

| | Finland | | | | Brazil | | | |
|---|---|---|---|---|---|---|---|---|
| Variable | Mean | SD | IQR | CV | Mean | SD | IQR | CV |
| Observed richness | 14.01 | 5.07 | 8.00 | 0.36 | 17.84 | 7.46 | 11.25 | 0.42 |
| Rarefied richness | 7.41 | 2.39 | 2.80 | 0.32 | 11.53 | 3.60 | 4.46 | 0.31 |
| Abundance | 886.57 | 700.73 | 852.00 | 0.79 | 181.50 | 111.38 | 190.00 | 0.61 |
| pH | 7.13 | 0.57 | 0.86 | 0.08 | 6.60 | 0.51 | 0.70 | 0.08 |
| Conductivity (µS/cm) | 88.17 | 84.19 | 86.90 | 0.95 | 55.79 | 58.68 | 29.00 | 1.05 |
| TN (µg/L) | 852.84 | 507.46 | 537.50 | 0.60 | 119.60 | 34.59 | 41.67 | 0.29 |
| TP (µg/L) | 72.14 | 58.52 | 65.67 | 0.81 | 15.33 | 12.47 | 9.30 | 0.81 |
| Stream width (m) | 3.84 | 2.53 | 2.95 | 0.66 | 2.60 | 1.75 | 0.84 | 0.67 |
| Shading (%) | 37.93 | 23.03 | 37.75 | 0.61 | 72.70 | 20.39 | 25.00 | 0.28 |
| Mean velocity (m/s) | 0.25 | 0.11 | 0.14 | 0.43 | 0.21 | 0.08 | 0.12 | 0.38 |
| Mean depth (m) | 0.18 | 0.07 | 0.07 | 0.37 | 0.13 | 0.07 | 0.07 | 0.54 |
| Substratum diversity | 1.06 | 0.33 | 0.39 | 0.31 | 1.29 | 0.20 | 0.25 | 0.16 |

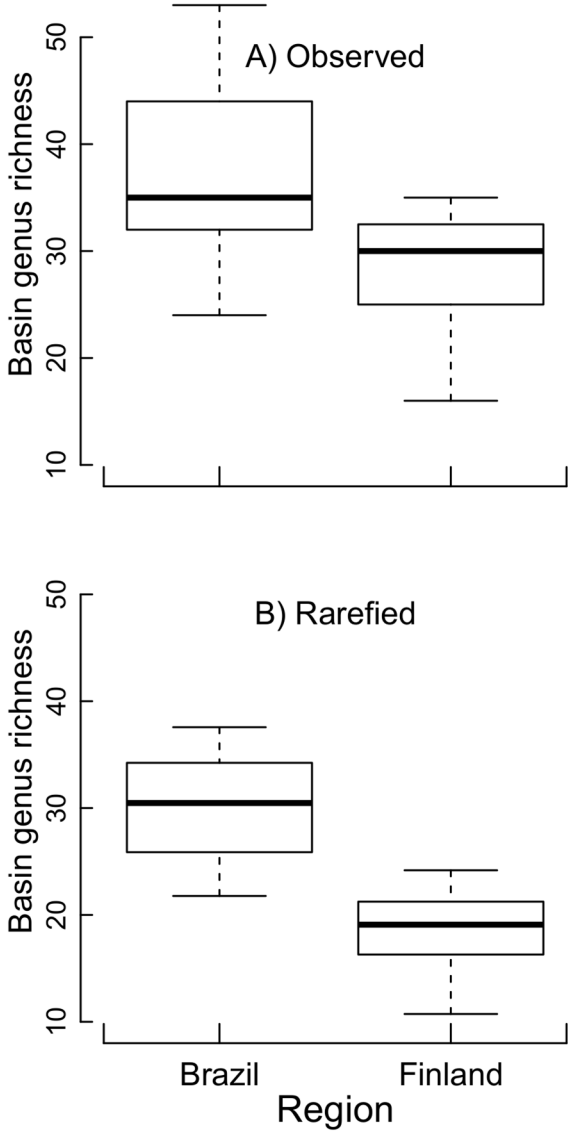
Table 2. Reduced multiple regression models showing the effects of 'region' and local environmental variables on rarefied richness (a; $F_{13,177} = 24.86$, $p < 0.001$), observed richness (b; $F_{13,178} = 17.88$, $p < 0.001$) and assemblage abundance (c; $F_{13,176} = 34.41$, $p < 0.001$) of stream insects in Finland and Brazil. Also shown are unique, common and total effects of each predictor variable from commonality analysis. See Supporting Information Table S1 for full models.

| a) Rarefied richness | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Estimate | SE | t | p | Unique | Common | Total | $R^2$ | adj. $R^2$ |
| (Intercept) | 5.504 | 0.792 | 6.946 | <0.001 | | | | | |
| region | 4.506 | 0.542 | 8.309 | <0.001 | 0.188 | 0.130 | 0.318 | | |
| width | 0.439 | 0.095 | 4.639 | <0.001 | 0.072 | -0.050 | 0.022 | | |
| forest cover | 1.654 | 0.679 | 2.438 | 0.016 | 0.020 | 0.085 | 0.105 | | |
| sand | -0.027 | 0.013 | -2.156 | 0.032 | 0.009 | 0.001 | 0.010 | | |
| total P | -2.388 | 1.204 | -1.983 | 0.049 | 0.013 | 0.016 | 0.029 | | |
| shading | 0.016 | 0.009 | 1.716 | 0.088 | 0.008 | 0.121 | 0.129 | | |
| | | | | | | | | 0.496 | 0.476 |
| b) Observed richness | | | | | | | | | |
| | Estimate | SE | t | p | Unique | Common | Total | | |
| (Intercept) | -0.609 | 5.394 | -0.113 | 0.910 | | | | | |
| region | 5.428 | 0.852 | 6.369 | <0.001 | 0.142 | -0.057 | 0.085 | | |
| width | 1.046 | 0.187 | 5.607 | <0.001 | 0.110 | 0.004 | 0.114 | | |
| forest cover | 4.368 | 1.382 | 3.160 | 0.002 | 0.035 | 0.057 | 0.092 | | |
| sand | -0.069 | 0.025 | -2.723 | 0.007 | 0.026 | 0.026 | 0.052 | | |
| pH | 11.654 | 6.060 | 1.923 | 0.056 | 0.013 | -0.012 | 0.001 | | |
| total P | -4.493 | 2.395 | -1.876 | 0.062 | 0.012 | 0.042 | 0.054 | | |
| | | | | | | | | 0.376 | 0.355 |
| c) Abundance | | | | | | | | | |
| | Estimate | SE | t | p | Unique | Common | Total | | |
| (Intercept) | 3.328 | 0.770 | 4.319 | <0.001 | | | | | |
| region | -1.186 | 0.149 | -7.971 | <0.001 | 0.141 | 0.301 | 0.442 | | |
| shading | -0.009 | 0.002 | -3.547 | <0.001 | 0.028 | 0.265 | 0.293 | | |
| pH | 2.820 | 0.801 | 3.518 | <0.001 | 0.027 | 0.018 | 0.045 | | |
| velocity | 2.097 | 0.599 | 3.498 | <0.001 | 0.027 | 0.116 | 0.144 | | |
| sand | -0.011 | 0.003 | -3.469 | <0.001 | 0.027 | 0.103 | 0.129 | | |
| pebble | 0.011 | 0.003 | 3.100 | 0.002 | 0.021 | -0.003 | 0.018 | | |
| particle diversity | 0.286 | 0.194 | 1.472 | 0.143 | 0.005 | 0.045 | 0.049 | | |
| forest cover | 0.274 | 0.189 | 1.455 | 0.147 | 0.005 | -0.002 | 0.002 | | |
| | | | | | | | | 0.610 | 0.592 |




698

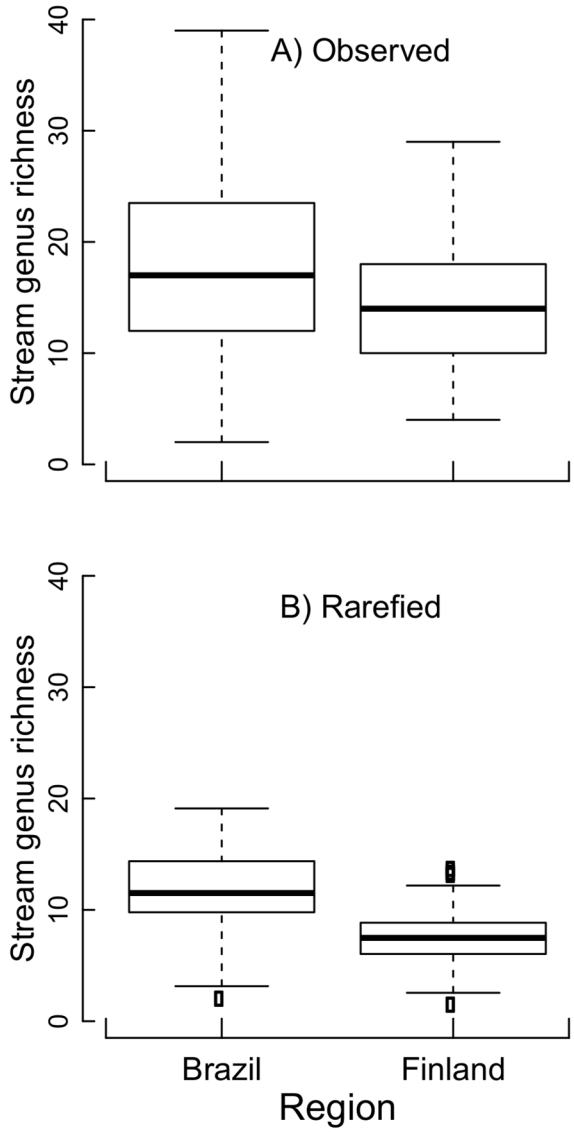
699 Fig. 1. Differences in regional stream insect genus richness between Brazil and Finland based
700 on similar-sized areas after random resampling in both regions. Note that a large number of
701 resampling analyses show the same pattern, i.e., regional genus richness is much higher in
702 Brazil than in Finland.




703

704 Fig. 2. Boxplots denoting differences in basin-scale stream insect genus richness between the
705 two regions, Brazil (N = 17 basins) and Finland (N = 19 basins). Shown are observed (A) and
706 rarefied (B) genus richness values.

707




708

709 Fig. 3. Boxplots denoting differences in local stream-scale genus richness between the two
710 regions, Brazil (N = 88 streams) and Finland (N = 97 streams). Shown are observed (A) and
711 rarefied (B) genus richness values.